Distribution of ant species along an altitudinal transect in continuous rainforest in subtropical Queensland, Australia

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Citation: Burwell, C.J. & Nakamura, A. 2011 12 20: Distribution of ant species along an altitudinal transect in continuous rainforest in subtropical Queensland, Australia. *Memoirs of the Queensland Museum — Nature* 55(2): 391-411. Brisbane. ISSN 0079-8835.

ABSTRACT

We present the distributions of ant species along an altitudinal gradient from 300 to 1100 m above sea level (m a.s.l.) within continuous rainforest in subtropical Queensland, Australia. Ants were collected along a single transect from four replicate plots at each of five zones of elevation (300, 500, 700, 900 and 1100 m a.s.l.) using a large array of methods targeting a wide range of microhabitats. These samples yielded a total of 170 ant species, represented by workers or ergatoid queens. A systematic ant sampling protocol, incorporating leaf litter extracts, spraying tree trunks with insecticide and hand collecting, was systematically conducted across all replicate plots in three seasons (spring, summer and autumn) enabling rigorous analysis of altitudinal patterns of species richness and assemblage structure. Species richness progressively declined with increasing altitude, with significant differences in the number of ant species between all zones except 300 and 500 m. Ant assemblages were significantly different among altitudinal zones with a progressive change in structure with increasing altitude between 300 and 900 m. Ant assemblages at 1100 m were markedly different to those at 900 m largely due to a dramatic decline in species richness rather than altitudinally restricted species. Short-term climate warming, therefore, may be of minor direct conservation concern for ants at this location. However, given the clear altitudinal signal of ant assemblages demonstrated here, ants have great potential as indicators of climate change-induced altitudinal range shifts. ❐ *ant species, Lamington National Park, IBISCA.*

Altitudinal stratification of assemblage structure is a generally accepted phenomenon for many invertebrate groups including moths (e.g. Brehm & Fiedler 2003; Brehm *et al.* 2007), butterflies (Fleishman *et al.* 2000; Wilson *et al.* 2007b), beetles (Monteith & Davies 1991; Escobar *et al.* 2005), flies (Wilson *et al.* 2007a), spiders (Monteith & Davies 1991; Chatzaki *et al.* 2005) and ants (Fisher 1999; Sanders *et al.* 2007). Many species of invertebrates are restricted to certain altitudinal ranges (Pyrcz & Wojtusiak 2002; Chatzaki *et al.* 2005; Botes *et al.* 2006), and some are only found at the upper limits of altitudinal gradients (Wilson *et al.* 2007a). These restricted altitudinal ranges have strong implications for assessing the impacts of climate change as upward shifts in distribution or complete disappearance of certain species at

higher altitudes are predicted to occur with increasing temperatures (Hodkinson 2005; Sanders *et al.* 2007).

In order to document differential responses of invertebrates to climatic changes, we need to establish baseline data describing the current altitudinal distributions of a wide range of invertebrate groups that may exhibit different ecological, evolutionary and physiological traits (Lomolino 2001; Calosi *et al.* 2008; Merrill *et al.* 2008). The IBISCA Queensland project was designed to document the current distributions of a range of invertebrate taxa along an altitudinal gradient within continuous rainforest in south-east Queensland. Specifically, the project aimed to identify taxa or suites of taxa that could be incorporated into long-term monitoring programs to detect the impacts of climate change. Here, we report on the altitudinal distribution of ants along the IBISCA transect.

Ant assemblages are known to be strongly stratified by altitude within a variety of vegetation and climatic zones, in both the northern and southern hemispheres (e.g. Fisher 1996; Samson *et al.* 1997; Bruhl *et al.* 1999; Sanders *et al.* 2003; Lessard *et al.* 2007). However, altitudinal studies of ants have largely focussed on the ground fauna, using pitfall trapping, litter extraction or a combination of both (e.g. Fisher 1999; Robertson 2002; Botes *et al.* 2006; Sanders *et al.* 2007). In contrast, we conducted specialist ant sampling which incorporated three methods (leaf litter extracts, spraying tree trunks with insecticide and hand collecting). This suite of methods targeted both ground and arboreal ants, as well as specialist nesters within and under rotting logs and rocks. Data from this systematic protocol were supplemented from ants collected using a large number of other methods employed during the IBISCA project.

The aims of the present study are broadly threefold. First, we establish an inventory of ant species along the altitudinal gradient of rainforest at Lamington National Park, using available data from all collecting methods used during the IBISCA project. This provides the most comprehensive baseline information on the altitudinal distribution of ant species within the region, where almost no ecological studies of ants have been previously conducted (but see Majer *et al.*, 2001). Secondly, we assess the effectiveness of our systematic protocol in sampling the ant fauna along the gradient. Thirdly, we analyse altitudinal patterns of ant species richness and assemblage structure to examine the utility of ants as bio-indicators of future climate change.

MATERIALS AND METHODS

Study site and design

The study site is a single altitudinal transect in the Green Mountains Section of Lamington National Park in the south-east corner of Queensland, Australia. The transect lies in continuous rainforest within the West Canungra Creek catchment. Climatic conditions vary along the transect, but at the Green Mountains National Park headquarters (approximately 940 m.a.s.l.) annual rainfall averages 1827 mm with most falling in summer. Average air temperatures range from a 4°C minimum in winter to 27°C maximum in summer. (see Kitching *et al.* 2011 for a detailed description of the transect).

Four experimental plots (A-D) were established at each of five zones of elevation; 300, 500, 700, 900 and 1100 m.a.s.l. (20 plots in total, see Kitching *et al.* 2011 for precise coordinates and elevations). Within each zone, plots were separated by at least 400 m. Forest structure and species composition varied along the transect (see Laidlaw *et al.* 2011). The low elevation plots (300 m a.s.l.) are located within *Araucaria* complex notophyll vine forest , the mid elevation plots (500-900 m a.s.l.) within complex notophyll vine forest and the 1100 m plots within simple microphyll fern forest dominated by Antarctic Beech, *Nothofagus moorei*. All plots had basaltic

soils derived from Cainozoic rocks. Each plot consisted of a central 20 m × 20 m quadrat and a surrounding circular survey area of 50 m radius measured from a metal stake located in the centre of the quadrat (see Kitching *et al.* 2011 for a detailed description of the experimental design).

SYSTEMATIC SAMPLING

Systematic sampling was designed to provide a robust measure of the overall ant fauna within a plot and was intended as a standard protocol that could be used for future monitoring of the impacts of climate change. Three systematic sampling methods targeted different elements of the ant fauna. Tullgren funnels (litter extracts) sampled the leaf litter fauna, spraying tree trunks with synthetic pyrethroid insecticide (bark sprays) sampled the arboreal fauna and timed bouts of hand collecting during the day (day hand) provided a general overview of the ant fauna while also sampling large species and specialist nesters rarely collected by the two previous methods. Systematic sampling involved the collection of one day hand sample, two litter extracts and two bark spray samples per plot in each sampling period. Systematic sampling was conducted at all elevations and plots in three periods each representing a different season: 16-27 October 2006 (spring), 8-20 March 2007 (autumn) and 17-29 January 2008 (summer). In summer 2008, bark sprays were conducted at two 1100 m plots on February 10 due to wet conditions during January.

Litter extracts

The two litter extracts per plot per season were collected from outside the central quadrat at opposite sides of the plot. Each extract was derived from 1 m^2 of leaf litter collected as four 50 cm × 50 cm squares at least 5 m distant from each other. Squares were not chosen randomly but consisted of areas with relatively uniform litter coverage. Thick rain-washed deposits of litter and soil were avoided. All litter and loose surface soil within the four squares was collected by hand, sieved with a litter sifter with a hexagonal mesh of chicken wire of approximately 15 mm in diameter. Litter extracts were transferred to a cloth bag and processed in Tullgren funnels within 24 hours of collection. Funnels were usually operated for 24 hours with a single 60 watt incandescent bulb, but wetter extracts were processed for up to 36 hours.

Bark sprays

Two bark spray samples were collected per plot per season from opposite sides of the plot. For each sample, five trees located outside the central quadrat were selected. Large trees (> 30 cm diameter at breast height (dbh)) were targeted, especially those encrusted with vines, epiphytes or moss. Their trunks were thoroughly sprayed using hand-held cans of pyrethroid insecticide (Mortein Fast Knockdown®), insecticide and the jet directed from the base to as far as possible up the trunk. Falling insects were collected on a rectangular sheet of rip-stop nylon (160 cm × 105 cm) placed at the base of each tree. Approximately 15 minutes after spraying, the five sheets were collected and their catches transferred to an ethanol filled vial using a suspended fabric funnel.

Day Hand Collecting

A single day hand sample was collected per plot per season. Ants were collected for 60 minutes by C.J. Burwell (CJB) within the 50 m radius of the plot, including the central quadrat. Day hand samples were collected between 0905 and 1650 hrs. Foraging workers on the ground, logs, foliage and tree trunks were collected. In addition, ant nests were searched for under rocks, within and under fallen logs and epiphytes and inside hollow branches and twigs. Not all observed worker ants were collected, rather the aim was to maximise the number of species collected.

TABLE 1. Summary of collection methods yielding supplementary ant samples examined in this study. See Ødegaard & Diserud (2011) for more detailed description of the beating and sampling methodology.

Method	Brief description of sampling methodology	Sampling period						Samples examined
		Oct.06	Jan.07	Feb.07	Mar.07	Jul.07	Jan.08	
Night hand	Each sample was a 30 min. bout of hand collecting at night (between 1830 and 2240 hrs), searching for active workers (not nests). Two or three samples collected per plot.	*			*		*	Oct & Mar: 300A, C; 500A-B; 700A-B; 1100C-D (no 500's in Oct). Jan.: 700A-D; 900A-D.
Malaise traps	One Townes Malaise trap per plot operated for 10 days.	*	*		*	*		All plots
Pitfalls	9 mm x 42 mm internal diameter cylindrical pitfall traps per plot, arrayed in a cross; open for 9 days; filled with 70% ethanol (Oct., Feb., Mar.) or propylene glycol (Jan.); 9 individual trap catches pooled into one sample.	*	*	*	*			All plots Jan. 300D sample lost.
Baited pitfalls	4 rectangular pitfall traps (125 mm x 87 mm) per plot, situated 25 m from central stake along main compass points; open for 10 days, each baited with wallaby dung (5 days) and mushrooms (5 days); catches from 4 traps pooled into one sample.	*	*			*		All plots
FIT – Flight intercept traps	One FIT per plot, operated for 10 days; each trap consisted of a vertical rectangular panel (66 cm x 70 cm) of layers of plastic kitchen wrap above a rectangular collecting container (14 cm x 66 cm) raised above ground level and filled with propylene glycol.	*	*		*			All plots
Yellow pans	Three yellow pans (rectangular plastic food containers approx. 165 mm x 110 mm) placed on ground within the central square, operated for three days per plot; catches from 3 traps pooled into one sample.	*			*			All plots
Baseline litter extracts	1 litre of unsifted leaf litter was collected from a single location within the central quadrat of each plot and extracted with a Tullgren funnel for 6 days.	*	*		*			All plots
Baseline bark sprays	1 m x 1 m squares of bark, at breast height, of living tree trunks within central quadrat were sprayed with synthetic pyrethroid insecticide and falling invertebrates collected on plastic sheets; 3-6 trees per plot were sprayed and their catches pooled into one sample.	*						300A-C; 500A, C; 700A-B; 900B-C; 1100A-C
Sweeping	15 minutes of sweeping low vegetation (40 cm internal diameter hoop size) per plot.	*			*			All plots
Beating	For each sample all vegetation (alive and dead) along a 20 m transect was beaten with a 1.5 m long stick and a 1 m x 1 m nylon beating sheet.	*						Miscellaneous samples from 300B-D; 700C; 900B-C.
Tuna baits	25 tuna baits each placed on the ground and on foliage within central quadrat of each plot; ants collected after 30 minutes; ants from all 50 baits pooled into one sample	*						All plots except 700C and 700D

Supplementary sampling

All other samples (i.e. those not systematically collected or not specifically targeting ants) containing ants were deemed supplementary samples, and were used to augment species richness and give a more comprehensive inventory for each plot. The samples included a small number of extra litter extracts, bark sprays and day hand samples collected in spring, summer and autumn, and a comprehensive set of litter extracts and bark sprays collected from all plots in winter 2007 (22-27 July). Additional supplementary samples were obtained from numerous other collection methods employed across a variety of plots and seasons (summarised in Table 1). The sampling effort employed at each plot and

TABLE 2. Summary of sampling 'intensity' (systematic and supplementary) across the five elevations (see Table 1 and text for definition of a sample for each collection method). Number of samples collected on the left of each cell; samples containing ants in parentheses. Total abundance (workers and ergatoid queens) for quantitative methods, total incidences (the occurrence of species within samples) and total species collected are collated for each method. *Beating was systematically undertaken across all elevations and plots, but only a small fraction of ants from beating samples were available for study.

Sampling method	Altitudinal Zone					Total abuncance	No. Incidences	No. species
	300 m	500 m	700 m	900 m	1100 m			
Systematic samples								
Litter extract	24 (24)	24 (24)	24 (24)	24 (24)	24 (22)	10297	942	78
Day hand	12 (12)	12 (12)	12 (12)	12 (12)	12 (12)	na†	834	100
Bark spray	24 (24)	24 (24)	24 (24)	24 (24)	24 (24)	3708	704	87
Supplementary samples								
Pitfall	15 (15)	16 (16)	16 (16)	16 (16)	16 (11)	4106	611	75
Night hand	10 (10)	4 (4)	21 (21)	25 (25)	8 (8)	na†	420	59
Baited pitfall	12 (12)	12 (12)	12 (11)	12 (12)	12 (11)	1795	385	83
Litter extract (non-systematic)	10 (10)	8 (8)	10 (10)	11 (11)	8 (8)	1450	238	48
Malaise	12 (12)	12 (10)	12 (12)	12 (10)	12 (6)	796	238	54
FIT	12 (12)	12 (10)	12 (11)	12 (11)	12 (6)	293	164	60
Baseline berlesate	12 (11)	12 (10)	12 (10)	12 (11)	12 (5)	362	119	32
Tuna baits	4 (4)	4 (4)	2 (2)	4 (4)	4 (3)	na†	108	33
Bark spray (non-systematic)	9 (8)	8 (7)	8 (7)	8 (6)	10 (6)	301	74	25
Sweeping	8 (5)	8 (6)	8 (7)	8 (4)	8 (1)	71	48	19
Baseline pyrethrum	3 (2)	2 (2)	2 (2)	2 (2)	3 (2)	279	47	26
Yellow pan	8 (7)	8 (6)	8 (7)	8 (5)	8 (2)	64	42	28
Day hand (non-systematic)	2 (2)	0	0	1 (1)	3 (3)	na†	35	26
Beating*	3 (3)	0	1 (1)	2 (2)	0	46	18	12
TOTAL samples	180 (174)	166 (155)	184 (177)	193 (180)	176 (130)			170

† Only incidences (not abundances) of species were recorded from samples collected with these methods and total ant abundances are not applicable (na).

the number of samples that yielded ants are summarised in Table 2.

Sorting and identification

This study is based on the occurrence of wingless workers and/or ergatoid queens of species within samples, as their presence is a reliable indication that those species are nesting within the plots. Winged or dealate reproductives however, may have dispersed from outside the confines of the plot. In addition, reproductives, especially males, could not always reliably be associated with their respective workers. Consequently, winged and delate reproductives have generally been ignored in this study, apart from six species for which they were the only castes collected.

Workers and ergatoid queens from all available IBISCA samples were processed and identified to morphospecies. Where possible, they were identified as described species using the published taxonomic literature, by comparison with type and critically identified specimens in the Australian National Insect Collection, or through the advice of, specialist taxonomists (Monomorium, Brian Heterick; Polyrhachis, Rudy Kohout). Unidentified taxa were assigned species codes that are specific to this project. A voucher collection of more than 3000 pinned ants, representing all species collected during the survey, is housed at the Queensland Museum. The generic classification used here follows Shattuck & Barnett (2001) and the subfamily classification follows Bolton (2003).

Data analysis

Ant assemblages were analysed as two datasets: ants from all samples (i.e. systematic and supplementary samples combined; for descriptive analyses only) and those from systematic samples alone (which allowed for fully balanced statistical analyses). Before analysis, ants collected from different sampling methods were pooled and their abundances were transformed to incidence (presence or absence) because some of the sampling methods (e.g. day and night hand collecting) only recorded the presence of species in samples. The unit of replication is a plot within each altitudinal zone (n=4), except for rarefaction curves where seasonal samples were treated separately to assess sampling sufficiency (n=12).

We first tested the sampling sufficiency of the systematic ant collecting protocol by generating sample-based rarefaction curves using the expected richness function (MaoTau) with EstimateS software ver. 8.0.0 (Colwell 2004). Sample-based rarefaction curves represent expected species richness, given n samples (n=12) for each altitudinal zone. The asymptote of each rarefaction curve was estimated with EstimateS using the Michaelis-Menten richness estimator (MM-Means). The shape of the rarefaction curve and the discrepancy between observed species richness and values of MM-Mean were used to evaluate sampling sufficiency at each altitudinal zone. Species richness of the local ant community within each altitudinal zone was estimated using the incidence-based coverage estimator (ICE). To test for differences in species richness among different altitudinal zones, single-factor ANOVA was performed with SPSS rel. 13.0 (SPSS Inc. 2004). For post-hoc pairwise comparisons we employed LSD tests. Inflation of type I error was not controlled as the risk of Type II error was high due to the small sample size at each altitudinal zone (n=4).

We used PRIMER ver. 5 (Clarke, 1993) to generate non-metric multi-scaling (NMDS) ordinations based on Sorensen similarity matrices calculated between each site pair, with 10 random restarts. NMDS ordinations were generated based on all samples (systematic plus supplementary) and systematic samples alone. The similarity between the two ordinations was compared using Mantel-type Spearman rank correlation on the similarity matrices (RELATE

TABLE 3. Generic distribution of 176 ant species recorded from the entire altitudinal transect. Species represented only by winged or dealate reproductives in parentheses. Genera marked with an asterisk contain at least one species considered to be characteristic of open forest, or likely to have been introduced to the plots via contamination of samples.

Genus	# spp.
MYRMECIINAE	
Myrmecia	2
CERAPACHYINAE	
Cerapachys	6
Sphinctomyrmex	2
AMBLYOPONINAE	
Amblyopone	2 (2)
Onychomyrmex	1
Prionopelta	1
HETEROPONERINAE	
Heteroponera	2
PONERINAE	
Cryptopone	2
Hypoponera	7
Leptogenys	5
Myopias	1 (1)
Pachycondyla	4
Platythyrea	1
Ponera	1
PROCERATIINAE	
Discothyrea	4
Probolomyrmex	1
ECTATOMMINAE	
Rhytidoponera	3
MYRMICINAE	
Anisopheidole	1
Cardiocondyla	(1)
Carebara	2
Colobostruma	4
Crematogaster	4
Eurhopalothrix	1
Lordomyrma	2
Machomyrma	1
Mayriella	3
Metapone	(2)
Monomorium	9
Myrmecina	1
Orectognathus	7
*Pheidole**	12
Podomyrma	9
Pristomyrmex	2
Rhopalomastix	1
Rhopalothrix	1
Solenopsis	1
Strumigenys	5
*Tetramorium**	1
FORMICINAE	
Acropyga	1
Camponotus	6
Myrmecorhynchus	2
Notoncus	2
Notostigma	1
Nylanderia	1
Paraparatrechina	3
*Paratrechina**	1
*Plagiolepis**	2
*Polyrhachis**	8
Prolasius	7
Stigmacros	4
Teratomyrmex	1
DOLICHODERINAE	
Anonychomyrma	2
Bothriomyrmex	1
*Iridomyrmex**	3
*Leptomyrmex**	4
*Ochetellus**	3
Tapinoma	4
*Technomyrmex**	2
Total genera	58
Total species	176

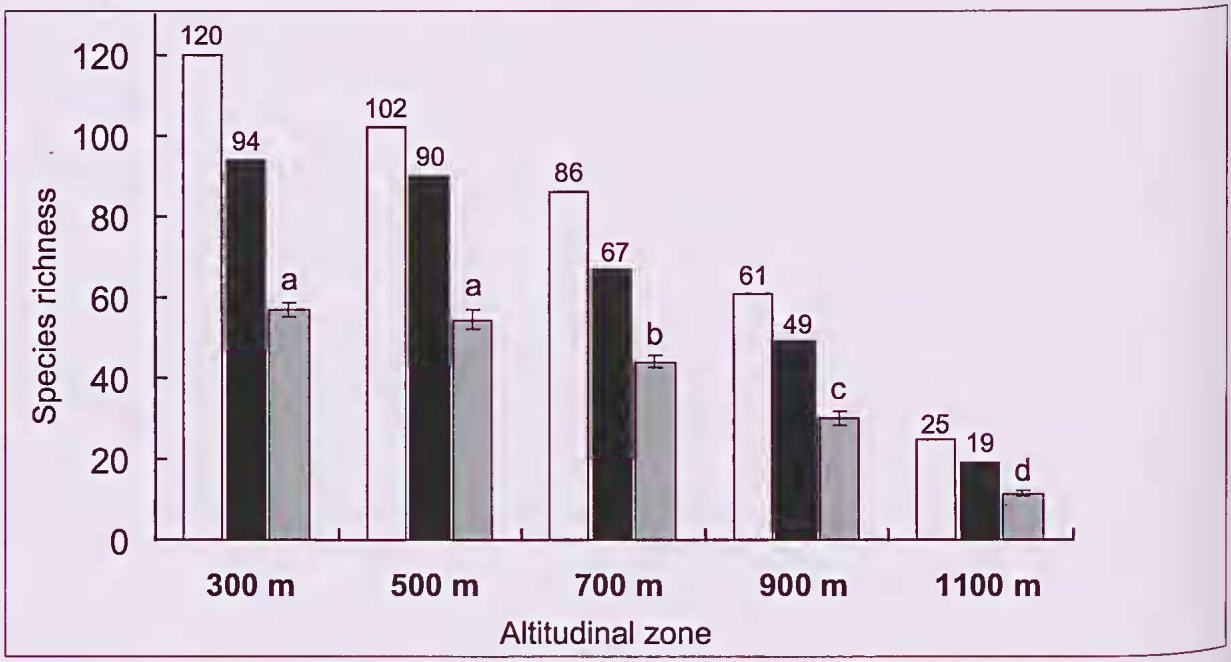

FIG. 1. Total species richness based on all samples (white bars) and systematic samples (black bars) with actual number of species shown above the bars. Mean species richness (with standard errors) based on systematic samples also shown with grey bars. Results of post-hoc LSD tests are shown with different letters indicating significant differences between altitudinal zones.

function in PRIMER), with 999 permutations. Non-metric multivariate ANOVA was performed with PERMANOVA software to test for differences in ant assemblage composition among altitudinal zones. This software executes multivariate ANOVA, using permutation methods, to calculate *P* values derived from pseudo *F* statistics of the distance measures (Anderson 2005). For each post-hoc pairwise test, PERMANOVA calculates the multivariate version of the *t*-statistic and Monte Carlo asymptotic *P* values which are not restricted by the number of unique permutations. Multivariate analyses were only carried out for systematic

TABLE 4. Numbers of shared species between altitudinal zones (above the diagonal) and unique species to each altitudinal zone (in the diagonal shown in bold), based on ant assemblages collected by all sampling methods. Numbers of shared and unique ant species derived from systematic sampling methods are shown in parentheses. Values below the diagonal are *t*-statistics calculated from post-hoc Monte Carlo permutation tests of PERMANOVA based on ant assemblages collected by systematic samples only. Larger values of *t*-statistic indicate greater dissimilarities in ant assemblage composition between altitudinal zones.

	300 m	500 m	700 m	900 m	1100 m
300 m	**41 (29)**	73 (60)	56 (41)	38 (30)	11 (5)
500 m	2.12	**7 (9)**	72 (56)	44 (36)	16 (13)
700 m	3.75	2.21	**6 (5)**	46 (35)	16 (12)
900 m	3.97	3.05	2.41	**5 (6)**	19 (12)
1100 m	5.92	5.09	5.51	4.01	**1 (4)**

All *t*-statistics are significant at $P<0.01$, except between 300 and 500 m where $P<0.05$.

TABLE 5. Comparison of the number of ant species (richness) collected at each study plot using both supplementory and systematic sampling methods (total) and systematic sampling methods only, with systematic richness expressed as a percentage of the total richness. Effectiveness of the systematic sampling methods averaged across the four plots within each altitudinal zone.

Elevation & Plot	Total richness	Systematic richness	% systematic vs total	Mean % (±SD) systematic vs total
300A	85	57	67.06	73.82 ± 4.67
300B	79	60	75.95	
300C	76	59	77.63	
300D	71	53	74.65	
500A	70	51	73.17	78.68 ± 4.89
500B	63	50	73.75	
500C	72	56	73.96	
500D	72	60	81.25	
700A	58	46	79.31	76.48 ± 4.40
700B	59	47	79.66	
700C	57	40	70.18	
700D	56	43	76.79	
900A	45	28	62.22	76.24 ± 9.77
900B	38	32	84.21	
900C	32	26	81.25	
900D	44	34	77.27	
1100A	14	10	71.43	73.17 ± 6.07
1100B	15	11	73.33	
1100C	18	12	66.67	
1100D	16	13	81.25	

samples as the dataset consisting of all samples suffers from seasonal and altitudinal sampling bias (see Tables 1 & 2).

RESULTS

Overall ant assemblage composition

A total of 170 ant species from 56 genera, represented by workers or ergatoid queens, were collected across the transect using all sampling methods (Table 3). An additional six species were represented only by winged or dealate reproductives. The altitudinal distributions of all species and their occurrence at the replicate plots within each elevational zone are summarised in Appendix 1. The majority of recorded species are known inhabitants of rainforest. However, a few species that were rarely collected (*Iridomyrmex* spp., *Ochetellus* spp., *Polyrhachis ornata*, *Plagiolepis* IBISCA2, *Leptomyrmex rufipes*) are likely to be transients from nearby open forest and a few species

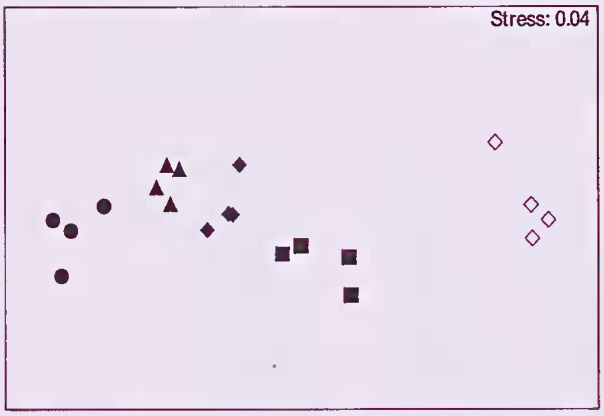

FIG. 2. NMDS ordinations based on ant assemblages collected from both systematic and supplementary samples (●, 300 m; ▲, 500 m; ◆, 700 m;■, 900 m; ◇, 1100 m). Ordinations were generated based on species' incidences (presence/absence) at a plot with data from all methods and seasons pooled.

associated with disturbed environments (*Pheidole megacephala*, *Pheidole* IBISCA8, *Tetramorium simillimum*, *Plagiolepis* IBISCA2, *Paratrechina longicornis*) were probably contaminants introduced with dung used in the baited pitfall trapping. However, the removal of these species from the overall dataset makes no appreciable differences in altitudinal patterns of species richness or assemblage structure and consequently they have not been excluded.

Using the complete dataset (all sampling methods combined) ant species richness peaked at the lowest elevation (300 m, 120 spp.) and progressively declined with increasing altitude (Fig. 1). Species richness was lowest at the highest elevation (1100 m, 25 spp.), dropping dramatically from that at 900 m (61 spp.). Ant assemblages were clearly correlated with altitude (Fig. 2). Replicate plots within each elevational zone formed distinct clusters on the NMDS ordination, with a progressive change in assemblages from the 300 to 900 m zones (Fig. 2). Paralleling the pattern for species richness, ant assemblages of the 1100 m plots were positioned along the altitudinal gradient, but were markedly separated from those of the 900 m plots (Fig. 2).

A total of 60 ant species were restricted to a single altitudinal zone, although more than half of these (31 spp.) were collected from single samples (effectively singletons). The 300 m zone had by far the most unique species, 41 including 20 'singletons'. All other zones had 7 or fewer unique species (Table 4) with only a single species (which was collected only once) unique to the 1100 m zone. The largest numbers of shared species were found between the 300 and 500 m (73) and 500 and 700 m (72) zones, while the least number of species was shared between 300 and 1100 m (11).

Ant assemblages from systematic sampling protocol

The systematic sampling protocol yielded a total of 143 ant species (represented by workers or ergatoid queens) across the entire transect, 84% of the 170 species represented by the complete dataset. At the level of the elevational zone, the systematic sampling methodology yielded between 76% and 88% of the complete inventory of species derived from all collecting methods. At the plot level, systematic samples yielded from 62% to 81% of the total species inventory (Table 5). However, when these values were averaged across the four plots within each altitudinal zone, the systematic sampling protocol yielded a remarkably consistent mean percentage of the plot species inventory (73-79%, Table 5).

For altitudinal zones at or above 700 m, rarefaction curves based on systematic samples (n=12) started to plateau (Fig. 3). Values of MM-Means were within the upper limit of 95% confidence intervals of accumulated species richness at the maximum number of samples, suggesting that the majority of species were collected from the plots within these altitudinal zones. For the 300 and 500 m altitudinal zones,

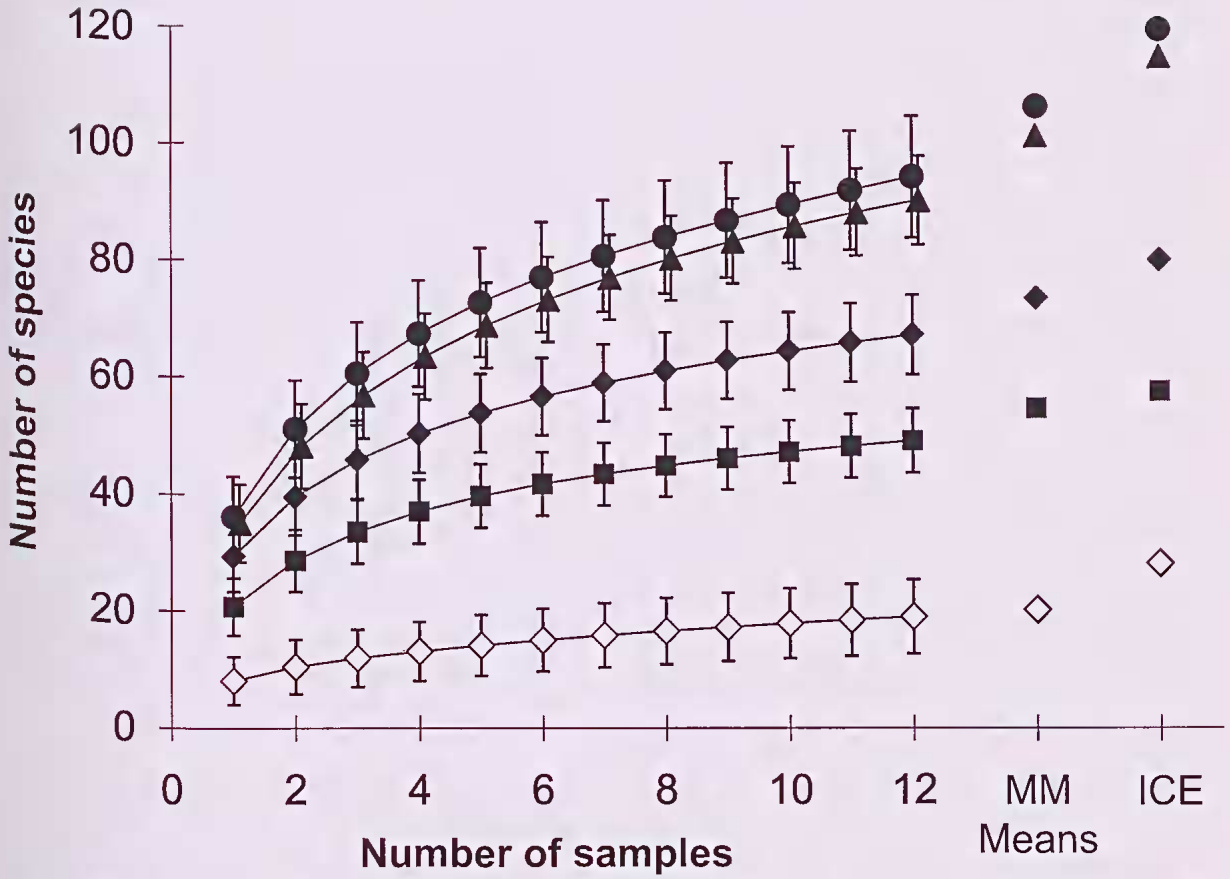

FIG. 3. Ant species rarefaction curves based on systematic samples. Rarefaction curves were generated for each altitudinal zone with 95% confidence intervals. (●, 300 m; ▲ 500 m; ◆ 700 m; ■, 900 m; ◇, 1100 m). Estimated species richness was also calculated using the asymptotic estimator (MM-Means) and the incidence-based coverage estimator (ICE) (see text for more details).

however, the terminal slopes of the rarefaction curves were noticeably steeper, with the values of MM-Means falling above the 95% confidence intervals. ICE predicted that the species richness of local ant communities would peak at 300 m altitudinal zone with 119 species, and would progressively decline with increasing altitude (115, 80, 57 and 28 species at 500, 700, 900, 1100 m respectively). These estimated species richness values were in broad agreement with the observed richness values based on all sampling methods, which yielded 120, 102, 86, 61 and 25 species at 300, 500, 700, 900, 1100 m respectively (Fig. 1). Species richness was significantly different among the altitudinal zones (ANOVA F=112.56, P<0.001) and post-hoc LSD tests indicated that species richness declined significantly from high to low altitudinal zones with the exception of 300 and 500 m, where no significant difference was found (Fig. 1).

The NMDS ordination based on systematic samples showed similar patterns to that based

on all samples (Mantel-type Spearman rank correlation: *Rho*=0.46, *P*<0.01. Ant assemblage compositions were significantly different between pseudo and F among altitudinal zones (PERMANOVA pseudo *F*=15.91, *P*<0.001) and post-hoc tests showed significant differences in all pairwise comparisons between zones (see also Table 5). The smallest differences in ant assemblage composition were found between 300 and 500 m (t = 2.117) and between 500 and 700 m (t = 2.207), and the greatest between 300 and 1100 m (t = 5.924).

DISCUSSION

This is the first study describing the altitudinal stratification of ants in Australia. In addition, it employs an extensive array of collecting methods targeting a very broad range of microhabitats. Despite the non-systematic nature of some sampling methods contributing to the complete dataset, the full inventory provides the most comprehensive information available on the distributions of ant species within rainforest along the altitudinal gradient. The significance of the complete inventory is reinforced by the generally consistent relationship between the observed total species richness (from systematic and supplementary samples) and values of ICE (estimated species richness derived from systematic samples) within elevations. The exception to this pattern was the 500 m zone where the observed species richness (102 spp.) was substantially lower than the estimated value (115 spp.), due perhaps to the lower number of samples (especially those from night hand collecting) taken there (Table 5).

Inevitably, our sampling protocols did not cover an exhaustive range of microhabitats. In particular, we may have missed species restricted to the upper canopy and perhaps those associated with tree hollows or the suspended soil of epiphytes. However, at least some of our methods, particularly bark spraying, Malaise traps and sweeping, probably collected canopy species foraging lower in trees. In addition, Majer *et al.* (2001) using canopy fogging within rainforest in the same study area, reported only 10-13 species of ants in two 10 × 10 m plots. In addition, we did not include methods to sample ants from deep within the soil. However, their inclusion is likely to have had little effect on observed patterns of assemblage structure as the fauna of strictly subterranean ants (e.g. Leptanillinae) probably consists of very few species.

Sampling sufficiency of the systematic protocol

Our systematic protocol sampled ants in a fully standardised manner from ground, arboreal and other specialised microhabitats, providing distributional data amenable to rigorous statistical analyses. However, compared to the complete dataset from all available samples, systematic samples underestimated the average species inventory per plot within each elevational zone by a substantial amount (21-27%). Despite these discrepancies in plot-based richness estimates, overall patterns of ant assemblage composition and richness across altitudinal zones were, nevertheless, consistent between systematic and complete datasets, suggesting the patterns found by the systematic sampling protocol are robust. We further scrutinised the sufficiency of systematic samples, using rarefaction techniques, to ensure that increased sampling intensity would not have changed the overall outcomes of the results. With respect to species richness, the shape of the rarefaction curves suggested potential undersampling at the lower altitudinal zones of 300 and 500 m.a.s.l. Increasing sampling intensity would have augmented species richness at these zones. However, values of the ICE and MM-means species richness estimators suggest that relative differences among altitudinal zones would likely be the same.

Species richness

We demonstrated that ant species richness was highest at low elevations and progressively declined above 500 m a.s.l. Similar monotonic declines in ant species richness with increasing altitude have been described for both tropical (Fisher 1996; Bruhl *et al.* 1999) and temperate regions (Lessard *et al.* 2007). However, more studies have found a mid-altitudinal peak in ant species richness with a subsequent decline at higher altitudes (Olson 1994; Samson *et al.* 1997; Fisher 1998; Fisher 1999; Sanders 2002; Sanders *et al.* 2003; Fisher 2004). Had we collected ants from even lower altitudes (i.e. 0-200 m) a mid-altitudinal peak may have emerged. However, we were unable to locate suitable sites as lowland rainforests have been extensively cleared, leaving only small rainforest remnants whose ant assemblages may not be directly comparable to that of continuous rainforest due to the effects of habitat fragmentation (Fahrig 2003).

Assemblage structure

Ant assemblage composition was significantly different among all altitudinal zones. On the NMDS ordinations, assemblage composition changed progressively with altitude, suggesting that neighbouring altitudes have more species in common than they have with other more distant altitudes. However, ant assemblages at the 1100 m plots were widely separated from those at 900 m, more than would be expected from an upslope shift of just 200 m. Ant assemblages at 1100 m were characterised by low species richness and almost no species occurred exclusively at this altitude. This dramatic change is perhaps related to the greater prevalence of cloud cover at the 1100 m plots. Vegetation communities also change dramatically from the 900 m plots (complex notophyll vine forest) to the 1100 m plots (simple microphyll fern forest). These marked changes in ant and vegetation communities may be related to increased levels of precipitation due to cloud-stripping at the highest elevations. Altitudinal studies in tropical rainforests outside Australia have also documented dramatic declines in the richness and abundance of ants at high elevations, associated with the transition into the zone of regular cloud formation (Samson *et. al.* 1997; Bruhl *et. al.* 1999). Many factors have been proposed to account for these observed declines, such as high humidity and soil moisture, low temperatures and solar radiation levels and a reduced leaf litter layer (Bruhl *et al.* 1999). Potential abiotic and biotic factors driving the structure of ant assemblages along this gradient will be the focus of future studies.

Faunal and floral assemblages occurring within the simple microphyll fern forest at the highest elevations at Lamington National Park are under most immediate threat due to climate warming. These areas are known to contain a number of altitudinally restricted and regionally endemic species, particularly invertebrates (Williams 2002). For example, Ødegaard and Diserud (2011), with respect to beetles, bugs and mutillid wasps associated with understorey vegetation, found that of the species unique to a single altitudinal zone, half were restricted to the 1100 m plots. In contrast, ant assemblages at 1100 m were characterised by low species richness and only a single species occurred exclusively at this altitude. Instead, most of the ant species unique to a particular altitudinal zone occurred at the lowest elevation, 300 m. Therefore, unlike many groups of invertebrates, the impacts of climate change may pose little conservation concern to ant species along the gradient in the short term.

Given the clear altitudinal signal of ant assemblages demonstrated here, it would appear that there is great potential to use ants to monitor altitudinal range shifts which may occur in response to increasing temperatures. Assemblage level responses to climate change have been demonstrated for butterflies in mountains in central Spain, where assemblages

with similar species composition have shifted uphill by approximately 300 m in around the last 30 years (Wilson *et al.* 2007b). The present study has established baseline data that will allow the detection of assemblage level responses of ants. Additionally, the replicated design of the IBISCA project can also enable rigorous statistical analyses to identify ant species that are indicative of particular altitudinal ranges. Monitoring of this suite of indicator species will facilitate the detection of differential species responses to climate change that may potentially obscure assemblage level responses.

ACKNOWLEDGEMENTS

Roger Kitching (Project leader), David Putland, Heather Christensen and all other IBISCA support staff and volunteers are thanked for their assistance during the project. Susan Wright, Geoff Thompson and Anna Marcora (Queensland Museum) are thanked for their huge efforts in conducting the systematic ant sampling. Other IBISCA participants, in particular, Geoff Monteith, Christine Lambkin, Kyran Staunton, Frode Ødegaard, Juergen Scmidl and Torsten Bitner provided access to the ants from their sampling programs. Finacial assistance was provided by a Queensland Government Smart State Grant, Griffith University, the Queensland Museum, Queensland Herbarium, SEQ Catchments Network and the Global Canopy Programme. Thanks also to Carla Catterall and other members of the WEDG discussion group for their helpful comments on the manuscript.

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APPENDIX 1. The distribution of ant species across the five altitudinal zones sampled during the IBISCA project, based upon all sampling methods and seasons. Letters indicate the replicate plots from which the species were recorded within altitudinal zone. Distributions based on the occurrence of wingless workers and ergatoid queens, except for the last six species which were represented only by alate or dealate queens.

Ant Species	Elevational zone				
	300 m	500 m	700 m	900 m	1100 m
Amblyopone australis	B D	A B C D	A B C D	A B C D	A B C D
Anonychomyrma QM3	A B C D	A B C D	A B C D	A B C D	B D
Hypoponera IBISCA1	A B	A B C D	B D	A B C D	C
Monomorium IBISCA4	A B C	A B C D	A B C D	A B C D	A B C D
Myrmecina QM1	B	A C	A B C D	A B C D	A B C D
Pheidole IBISCA2	A B C D	A B C D	A B C D	A B C D	C
Sphinctomyrmex IBISCA1	A B	C	C	D	C
Tapinoma IBISCA4	A B	A C	C	B	B
Pheidole IBISCA8	D		C	B	C D
Amblyopone IBISCA1	D			B	A
Tapinoma IBISCA3	A C				C
Anonychomyrma IBISCA1	A B C D	A B C D	A B C D	A C D	
Camponotus IBISCA3	C	B D	A B C	A C D	
Carebara IBISCA1	A B C D	A B C D	A B C D	A D	
Crematogaster IBISCA1	A B C D	A B C D	A B C D	A B C D	
Discothyrea IBISCA3	A B C D	A B C D	A B C	A	
Hypoponera IBISCA2	A B C D	A B C D	A B C D	B C D	
Hypoponera IBISCA3	B	A B	B C	A B	
Hypoponera IBISCA4	A B	A B	A B C	A B D	
Leptogenys hackeri	A B C	A	A B C D	A D	
Leptomyrmex cnemidatus	A B C D	A B C D	A B C D	A B C D	
Leptomyrmex nigriventris	A B C D	C D	A B C D	A B D	
Mayriella abstinens	A B C D	A B C D	A B C D	D	
Mayriella overbecki	A B D	A B C D	A B C D	A D	
Monomorium tambourinense	A B C D	A B C D	A B C D	A B C D	
Notostigma foreli	A B C D	C D	A B C	A	
Orectognathus versicolor	A B C D	A B C D	A B C D	A D	
Pheidole IBISCA1	A B C D	A B C D	A B C D	A B C D	
Pheidole IBISCA3	B D	A B C D	A B C D	A B D	
Polyrhachis IBISCA1	A B C D	A B C D	A B C D	A D	
Polyrhachis IBISCA3	A B C D*	B C D	C	A B	
Ponera leae	A B C	B C D	A B C D	A B C D	

APPENDIX 1. continued ...

Ant Species	Elevational zone				
	300 m	500 m	700 m	900 m	1100 m
Prionopelta robynmae	A B C D	A B C D	A B C D	A D	
Pristomyrmex quadridentatus	A B	A B C	A B C D	A C D	
Pristomyrmex wheeleri	B C	A	B	A D	
Rhytidoponera croesus	A B	A B C D	A B C D	A B C D	
Solenopsis IBISCA1	A B C D		A D	A B C D	
Hypoponera IBISCA6	A B	B		C D	
Pheidole megacephala	A C D	A B		B	
Anillomyrma IBISCA1	A B C D	A B C D	A B C D		
Cerapachys IBISCA2	A B	A C D	C		
Heteroponera IBISCA2	A B C	A C D	B C		
Iridomyrmex IBISCA2	B	A	D		
Leptogenys anitae	A B C D	A B C D	A B C D		
Notoncus capitatus	A B C D	A B C D	A D		
Orectognathus rostratus	B C D	A C D	A		
Paraparatrechina IBISCA2	A B C D	A B C	A		
Pheidole IBISCA4	A B C D	A B C D	A		
Pheidole IBISCA6	A B C D	A B C D	D		
Podomyrma IBISCA2	A B C D	A B D	A B		
Podomyrma IBISCA8	A B C	B	A		
Polyrhachis IBISCA4	A D	A	A B C D		
Prolasius IBISCA3	A B C D	A B C D	A B		
Rhytidoponera chalybaea	A B C D	A B C D	A B C D		
Rhytidoponera victoriae	A B C D	A B C D	A B C D		
Stigmacros major	A C D	A C	B C		
Strumigenys denteras	B C	A B D	A		
Technomyrmex IBISCA1	A B C	A C D	A B C D		
Orectognathus phyllobates	C D		A B		
Podomyrma IBISCA5	A		A C D		
Camponotus mackayensis	A B C D	A B C D			
Carebara IBISCA2	A B C D	B C D			
Colobostruma biconvexa	A C D	C			
Leptogenys mjobergi	A B C	A B C D			
Leptomyrmex burwelli	A B C D	A B C D			
Lordomyrma IBISCA1	A B	C D			
Monomorium IBISCA5	A B C D	D			

APPENDIX 1. continued ...

Ant Species	Elevational zone				
	300 m	500 m	700 m	900 m	1100 m
Monomorium IBISCA6	B	D			
Pachycondyla porcata	A B C D	C D			
Nylanderia IBISCA1	A B C D	A B C D			
Pheidole IBISCA7	A B C D	D			
Platythyrea parallela	A C D	C			
Podomyrma IBISCA3	A D	A B D			
Prolasius IBISCA5	A B C D	D			
Prolasius IBISCA7	A B	B D			
Rhopalomastix IBISCA1	A C	B			
Rhopalothrix orbis	A C D	B			
Stigmacros barretti	C	B C D			
Tapinoma IBISCA1	B C D	A B C D			
Acropyga pallida	A B C				
Anisopheidole IBISCA1	A C D				
Camponotus IBISCA1	B C D				
Camponotus IBISCA2	A D				
Camponotus IBISCA4	A C				
Cerapachys IBISCA1	A				
Cerapachys IBISCA4	A D				
Cerapachys IBISCA5	C				
Cerapachys IBISCA6	B				
Colobostruma sisypha	B C				
Crematogaster IBISCA2	A B D				
Crematogaster IBISCA3	A B C D				
Crematogaster IBISCA4	A				
Eurhopalothrix australis	A				
Iridomyrmex IBISCA1	B D				
Iridomyrmex IBISCA3	A				
Leptogenys sjostedti	A B C D				
Leptomyrmex rufipes	D				
Lordomyrma IBISCA2	A				
Mayriella spinosior	A B C D				
Myrmecia nigrocincta	A B C				
Ochetellus IBISCA1	D				
Ochetellus IBISCA3	C				

APPENDIX 1. continued ...

Ant Species	Elevational zone				
	300 m	500 m	700 m	900 m	1100 m
Orectognathus mjobergi	A				
Orectognathus robustus	B				
Pachycondyla australis	A C D				
Paraparatrechina IBISCA3	A D				
Paratrechina longicornis	D				
Pheidole IBISCA10	A B C D				
Pheidole IBISCA9	B				
Plagiolepis IBISCA2	D				
Podomyrma IBISCA6	B				
Podomyrma IBISCA7	D				
Polyrhachis IBISCA5	C D				
Polyrhachis IBISCA6	C				
Polyrhachis clio	C D				
Polyrhachis ornata	B				
Polyrhachis pilosa	A C D				
Probolomyrmex greavesi	C				
Stigmacros IBISCA2	A				
Stigmacros IBISCA4	C				
Cryptopone IBISCA1		A B	A B C D	A B C D	A B C D
Prolasius IBISCA1		A B C D	A B C D	A B C D	A B C D
Strumigenys perplexa		B C D	A B C D	A B C D	A B C D
Cryptopone IBISCA2		C	B		C
Discothyrea IBISCA1		A B C D	B C D		C
Heteroponera IBISCA1		C D	B C		A B D
Monomorium IBISCA1		A B D	D		A C D
Prolasius IBISCA6		D		A B C	A B C D
Monomorium nigriceps		A	B	A D	
Myrmecorhynchus IBISCA1		A B C D	A B C D	A B C D	
Paraparatrechina IBISCA4		A B C D	B C D	B D	
Prolasius convexa		A B C D	A B C D	A B C D	
Onychomyrmex IBISCA1		D		D	
Cerapachys IBISCA3		C D	D		
Hypoponera IBISCA5		A C D	D		
Hypoponera IBISCA7		A B	D		
Ochetellus IBISCA2		A	B		

APPENDIX 1. continued ...

Ant Species	Elevational zone				
	300 m	500 m	700 m	900 m	1100 m
Pheidole IBISCA5		A B C	A B C D		
Prolasius IBISCA2		A C D	A B C D		
Strumigenys harpyia		A B C D	A B C D		
Tapinoma IBISCA2		A B	A B		
Teratomyrmex greavesi		A C	A		
Bothriomyrmex IBISCA1		A			
Camponotus IBISCA5		C			
Colobostruma froggatti		C			
Discothyrea IBISCA4		C D			
Machomyrma IBISCA1		D			
Plagiolepis IBISCA1		C D			
Podomyrma IBISCA4		A C			
Colobostruma australis			C	C D	
Orectognathus antennatus			A B C D	A B C D	
Podomyrma IBISCA1			A B C	B C D	
Sphinctomyrmex IBISCA2			D	B	
Monomorium IBISCA3			A B C D		
Myopias chapmani			D		
Podomyrma IBISCA9			D		
Strumigenys belua			A		
Strumigenys tisisyx			D		
Tetramorium simillimum			D		
Discothyrea IBISCA2				A C D	A B C D
Monomorium IBISCA2				B	A B C D
Myrmecorhynchus IBISCA2				A B C	A B D
Notoncus spinisquamis				A B	B C D
Technomyrmex IBISCA2				A D	A B
Leptogenys excisa				C	
Myrmecia brevinoda				A	
Orectognathus elegantulus				A B D	
Pachycondyla pachynoda				A B C	
Pheidole IBISCA12				C	
Pachycondyla IBISCA3					D

APPENDIX 1. continued ...

Ant Species	Elevational zone				
	300 m	500 m	700 m	900 m	1100 m
Queens only					
Amplyopone IBISCA2 *	B				
Amplyopone IBISCA3*		B			
Cardiocondyla IBISCA1*		A		A B	
Metapone IBISCA1*	B C D			D	
Metapone IBISCA2*		D			
*Myopias tasmaniensis**		C			